Kennedy, P., & Radford, A. N. (2020). Sibling quality and the haplodiploidy hypothesis. *Biology Letters*, *16*(3), [20190764]. https://doi.org/10.1098/rsbl.2019.0764

Sibling quality and the haplodiploidy hypothesis

P. Kennedy & A. N. Radford
School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, BS8 1TQ, UK

The 'haplodiploidy hypothesis' argues that haplodiploid inheritance in bees, wasps, and ants generates relatedness asymmetries that promote the evolution of altruism by females, who are less related to their offspring than to their sisters ('supersister' relatedness). However, a consensus holds that relatedness asymmetry can only drive the evolution of eusociality if workers can direct their help preferentially to sisters over brothers, either through sex-ratio biases or a pre-existing ability to discriminate sexes among the brood. We show via a kin selection model that a simple feature of insect biology can promote the origin of workers in haplodiploids without requiring either condition. In insects in which females must found and provision new nests, body quality may have a stronger influence on female fitness than on male fitness. If altruism boosts the quality of all larval siblings, sisters may therefore benefit more than brothers from receiving the same amount of help. Accordingly, benefits of altruism would fall disproportionately on supersisters in haplodiploids. Haplodiploid females should be more prone to altruism than diplodiploid females or males of either ploidy when altruism elevates female fitness especially, and even when altruists are blind to sibling sex.

Eusociality | Haplodiploidy | Altruism

In 1964, W. D. Hamilton proposed that haplodiploidy has been a major driving force behind the multiple origins of eusociality in the Hymenoptera (bees, wasps, and ants) [1,2]. Males are haploid, inheriting genes only from the mother, whilst females are diploid, inheriting genes from both parents [3]. In monogamous haplodiploids, sisters share their entire haploid father's genome, whilst maternal alleles have a 50:50 chance of being shared by sisters. Accordingly, a female is related to her sisters by $r = 0.75$ (*i.e.,* 0.5 from the father and 0.5 *x* 0.5 from the mother). This 'supersister' relatedness is 50% greater than a female's relatedness to her own offspring ($r = 0.5$), suggesting that a female should prefer to raise sisters than attempt personal reproduction [1,2,4].

The haplodiploidy hypothesis has been repeatedly questioned [5–13], and other reasons for a possible link between haplodiploidy and female altruism have been suggested in its place (e.g., [14–16]). Theoretical objections have largely centered on the problem that the haplodiploidy hypothesis requires helper females to bias altruism towards sisters (sister-biased helping). If altruism is received equally by sisters and brothers, haplodiploids should be no more prone to eusociality than diplodiploids (in which both sexes are diploid and produced sexually). This is because, under haplodiploidy, a female's

relatedness to brothers is only $r = 0.25$: indiscriminate sibling altruism will produce an average recipient relatedness of $r = 0.5$. Under both haplodiploidy and diplodiploidy, then, there would be no asymmetry in relatedness to offspring and siblings. Trivers and Hare [8] argued that sister-biased helping could arise if helpers tend to inhabit nests with a female-biased brood sex ratio, but noted that an increasingly female bias in the population diminishes the value of rearing sisters and amplifies the value of rearing brothers. Accordingly, female sex-ratio biases in nests with helpers must be more extreme than elsewhere in the population ('split sex ratios') for altruism to be promoted more by haplodiploidy than by diplodiploidy [8,17]. Because split sex ratios arise only under rare and often complex conditions [5], this requirement led to a consensus that the haplodiploidy hypothesis is an unlikely driver of eusociality. Recently, Rautiala *et al.* [18] have argued that split sex ratios are unnecessary, and haplodiploidy can drive eusociality at all sex ratios – on the crucial assumption that the first-evolving workers discriminate among brood by directing their help preferentially towards females (*'the ability for helpers to treat sisters and brothers differently'*; [18]). Although sex discrimination occurs in simple eusocial species (*e.g.*, [19]) and is familiar in more advanced eusocial taxa [20,21], it remains unknown whether this ability evolved subsequent to the evolution of workers or characterized workers at the dawn of sociality.

Here, we highlight a scenario in which the classic haplodiploidy effect [1] can drive eusociality without split sex ratios and without females needing to treat developing sisters and brothers differently. Models of eusocial evolution have focused on the *quantity* of siblings raised by helpers [8,18,22], but recent empirical studies of facultatively and primitively social insects have found that effects on sibling quantity alone can be too small to drive voluntary altruism [23,24]. We suggest a need to incorporate additional effects that helpers may have on the *quality* of siblings.

Across vertebrates and insects, the reproductive successes of males and females can depend differently on body condition [25,26], which can be influenced by the receipt of resources from helpers before reproductive maturity [27]. There has been no systematic and direct comparison of the extent to which male versus female fitness depends on body condition in nest-founding insects, and so the strength and sex-asymmetry of condition-dependence remains largely unknown. However, greater condition-dependent variability in female fitness may plausibly arise when female nest-founding (including larval provisioning and any necessary female-only overwinter survival) is energetically challenging [27–30], and especially in contexts involving relatively limited scope for male–male competition or mate choice [29]. In nest-founding insects without biparental care, a female must face the extreme challenge of founding a new nest and raising larvae to adulthood [31] in addition to mating; a male must only mate. Empirical results suggest that higher-condition females (larger, with more fat reserves acquired during development) have a stronger chance than those in poorer condition of being

successful nest-builders [32,33], and reveal heavy reliance on energy reserves by foundress females [31,34].

Using a kin selection model, we explore whether female-biased condition-dependence alters thresholds for eusociality under different ploidies. We focus on a situation requiring minimal assumptions about worker phenotypes: we assume (1) that the ability to discriminate male and female brood [18] is absent, (2) that there are no pre-existing biases in the ability of males and females to provide help [22], and (3) that mothers retain control over their broods' sex ratios. Helpers may increase the condition of all brood, which is likely to benefit females disproportionately. In this context, we find that a helper should not only aim to amplify the quantity of siblings but also to elevate the quality of sisters, maximising the quantity of nieces and nephews.

Model

We assume a monogamous, outbreeding population. We build on the framework of Davies *et al*. [22], who analyse the evolution of eusociality under different ploidies, to incorporate sex-asymmetrical condition-dependence. Females develop to be sterile helpers with probability x (with a population average $\bar{x}$), males develop to be sterile helpers with probability y (with a population average $\bar{y}$), and the brood sex ratio (the proportion male) is z (with a population average $\bar{z}$). Help h is the sum of help from male and female helpers. We allow altruists to influence two different (not mutually exclusive) components of the fitness of brood in the nest. First, helpers may raise the probability $B = B(h)$ that brood survive to reproductive maturity (*i.e.*, helpers may raise the quantity of adult reproductive siblings). We follow Davies *et al*. [22] in denoting the fitness effect of female help on relative brood survival to reproductive maturity as $b_{\mathrm{F}} = e_{\mathrm{F}} \frac{dB}{dh}\Big|_{h=\bar{h}} / B(\bar{h})$, where e_{F} denotes helping efficiency of females and $B(\bar{h})$ is the population-average survival to reproductive maturity. Likewise, $b_{\mathrm{M}} = e_{\mathrm{M}} \frac{dB}{dh}\Big|_{h=\bar{h}} / B(\bar{h})$ denotes the fitness effect of male help on relative brood survival to reproductive maturity, where e_{M} denotes helping efficiency of males. Second, helpers may raise the probability $Q = Q(h)$ that, given a female brood-member has reached reproductive maturity, she will successfully found a new nest (helpers therefore may influence the quality of adult reproductive sisters). We let the fitness effect of female help on female relative nest-founding success be $q_{\mathrm{F}} = e_{\mathrm{F}} \frac{dQ}{dh}\Big|_{h=\bar{h}} / Q(\bar{h})$, where $Q(\bar{h})$ is the population-average nest-founding success. Likewise, $q_{\mathrm{M}} = e_{\mathrm{M}} \frac{dQ}{dh}\Big|_{h=\bar{h}} / Q(\bar{h})$ denotes the fitness effect of male help on female relative nest-founding success. Nest-founding success is a female-

specific trait, affected by the amount of help a nest-founding female receives before her own reproductive maturity.

In the Supplementary Information, we show that selection favours a small increase in female helping when:

$$(b_{\mathrm{F}} + q_{\mathrm{F}})(1-\bar{x})(1-\bar{z})v_{\mathrm{F}}p_{\mathrm{sis|F}} + b_{\mathrm{F}}(1-\bar{y})\bar{z}v_{\mathrm{M}}p_{\mathrm{bro|F}} > v_{\mathrm{F}}p_{\mathrm{self|F}} \quad (1)$$

where consanguinities (p) denote the probabilities with which a random allele in the social partner is identical by descent to a random allele at the same locus in the actor [35]. Assuming monogamy, haplodiploid consanguinities from a focal female are $p_{\mathrm{self|F}} = \frac{1}{2}$ to self, $p_{\mathrm{sis|F}} = \frac{3}{8}$ to a sister, and $p_{\mathrm{bro|F}} = \frac{1}{4}$ to a brother [5]. Diplodiploid consanguinities are $p_{\mathrm{self|F}} = \frac{1}{2}$ to self, $p_{\mathrm{sis|F}} = p_{\mathrm{bro|F}} = \frac{1}{4}$ to siblings. Reproductive females and reproductive males have individual reproductive values v_{F} and v_{M} respectively (a measure of the probability with which males and females contribute to the distant future gene pool; see Supplementary Information). The indirect fitness benefits of developing as a sterile altruist are on the left-hand side of inequality 1. The direct fitness cost (the loss of the focal individual's own opportunity to reproduce, valued at $v_{\mathrm{F}}p_{\mathrm{self|F}}$) is on the right-hand side. The actor's sacrifice results in $b_{\mathrm{F}}(1-\bar{x})(1-\bar{z})$ additional reproductive sisters and $b_{\mathrm{F}}(1-\bar{y})\bar{z}$ additional reproductive brothers, and an addition of nieces and nephews equal in value to $q_{\mathrm{F}}(1-\bar{x})(1-\bar{z})$ reproductive sisters.

Holding b_{F} fixed, the threshold benefit levels in terms of improvements to sister quality required to drive a small rise in helping by females are for haplodiploids and diplodiploids respectively:

$$q_{\mathrm{HapF}} = \frac{2}{3}\left(\frac{2}{(1-\bar{x})(1-\bar{z})} - 2b_{\mathrm{F}}\right) \quad (2)$$

$$q_{\mathrm{DipF}} = \frac{2}{(1-\bar{x})(1-\bar{z})} - 2b_{\mathrm{F}} \quad (3)$$

In a nonsocial population ($\bar{x} = \bar{y} = 0$) with an even sex ratio ($\bar{z} = \frac{1}{2}$), q_{HapF} and q_{DipF} can be interpreted as the number of additional nephews and nieces (resulting from the sibling quality-boosting effect of becoming a sterile altruist) required to promote the initial invasion of altruists.

Next, we evaluate the costs and benefits of altruism (y) by males. Solving for the fitness effects (see Supplementary Information), selection favours a small increase in male altruism when, for both diplodiploid and haplodiploid males:

$$(b_{\mathrm{M}} + q_{\mathrm{M}})(1-\bar{x})(1-\bar{z})v_{\mathrm{F}}p_{\mathrm{sis|M}} + b_{\mathrm{M}}(1-\bar{y})\bar{z}v_{\mathrm{M}}p_{\mathrm{bro|M}} > v_{\mathrm{M}}p_{\mathrm{self|M}} \quad (4)$$

Assuming monogamy, diplodiploid consanguinities from a focal male are $p_{\mathrm{self|M}} = \frac{1}{2}$, $p_{\mathrm{sis|M}} = p_{\mathrm{bro|M}} = \frac{1}{4}$, whilst haplodiploid consanguinities are $p_{\mathrm{self|M}} = 1$, $p_{\mathrm{sis|M}} = \frac{1}{4}$, and $p_{\mathrm{bro|M}} = \frac{1}{2}$. Holding b_{M} fixed, the threshold benefit level in terms of sister quality required to drive a small rise in helping by males of either ploidy is:

$$q_{\mathrm{HapM}} = q_{\mathrm{DipM}} = \frac{2}{\bar{z}(1-\bar{y})} - 2b_{\mathrm{M}} \tag{5}$$

Thus, for instance, consider a nonsocial population ($\bar{x} = \bar{y} = 0$) with unbiased sex ratios ($\bar{z} = \frac{1}{2}$), in the case where helpers will have no effect on the quantity of siblings produced ($b_{\mathrm{F}} = b_{\mathrm{M}} = 0$). The thresholds for the invasion of altruism (due to the effects of sex-indiscriminate helping increasing female quality) are:

$$\begin{cases} q_{\mathrm{HapF}} = 2.\dot{6} & \text{for haplodiploid females} \\ q_{\mathrm{DipF}} = 4 & \text{for diplodiploid females} \\ q_{\mathrm{HapM}} = q_{\mathrm{DipM}} = 4 & \text{for males of either ploidy} \end{cases}$$

These thresholds can be understood in terms of life-for-life relatednesses [5]: when $\bar{z} = \frac{1}{2}$, life-for-life relatedness to a sister's offspring (nephews and nieces) is 0.375 for a haplodiploid female but 0.25 for a diplodiploid female. Life-for-life relatedness to oneself is 1. To break even when sacrificing her reproduction, a haplodiploid female's altruism must then result in $\frac{1}{0.375} = 2.\dot{6}$ additional nieces and nephews through the improved quality of her reproductive sisters, but a diplodiploid female's help must result in $\frac{1}{0.25} = 4$ additional nieces and nephews. A smaller boost to the quality of sisters (q_{F}) is required to justify altruism for haplodiploid females than for other actor types, unless altruists are able to provide a sufficient boost to sibling quantity (b_{F} and b_{M}) to make boosts to sibling quality unnecessary ($q_{\mathrm{F}} = 0$, which occurs at $b_{\mathrm{F}} = 2$ for the initial invasion of altruists; **Fig. 1a**). The benefit thresholds for haplodiploid females (dashed lines in **Fig. 1b**, q_{HapF}) are lower than those required for diplodiploid females (solid lines in **Fig. 1b**, q_{DipF}) throughout the invasion of altruists ($\bar{x}$ ranging from 0 to 1).

As helpers evolve, mothers are expected to bias offspring sex ratios in favour of the more helpful sex [15,22]. We therefore plot the coevolution of sex ratios and female altruism in **Fig. 1c-f**. When help boosts sister quality especially, haplodiploids can evolve female altruism when diplodiploids cannot (**Fig. 1c-d**). When the boost to sister quality is enough to drive altruism in diplodiploids, haplodiploids evolve a higher level of female altruism than diplodiploids (**Fig. 1e-f**).

Discussion

We find that haplodiploid females enjoy lower thresholds for altruism, in comparison to either diplodiploid females or males of either ploidy, on the condition that staying to provision the brood increases the quality of sisters more than that of brothers (Fig. 2). This effect arises even in the absence of split sex ratios [8] or helpers preferentially biasing help towards one sex in the brood [18]. A major bottleneck in the success or failure of a primitive social insect colony may be the hopeful queen's nest-founding quality, affected by the level of help she received in her own development. This is similar to the effects of sunk-cost hysteresis in economics [36]: initiating a new nest (a firm entering the market) demands a huge expenditure of effort, but maintaining an established nest (a firm trading in the market) is relatively easier. At the dawn of sociality, a large effect of workers' help may in principle not be visible until the following generation, as higher levels of worker help may result in more successful future nest-founding by sibling queens.

A role for sex-asymmetrical condition-dependence has previously been proposed for the haplodiploidy hypothesis. In this verbal 'synergism model', Frank and Crespi [27] suggest that Trivers-Willard effects [26] drive split sex ratios. First, helpers increase sibling condition. Then, mothers with helpers evolve to adjust sex ratios towards daughters, who benefit most from high condition. Resulting split sex ratios increase selection for helping (by increasing recipient relatedness). The synergism model assumes that helpers have already evolved (and so can explain their maintenance and spread but not origin), and the necessity of split sex ratios has been challenged [18]. Our model shows that condition-dependence can also play a more fundamental role, not only amplifying the spread of altruism by haplodiploid females [27] but driving its origins in populations without sex-ratio biases.

Empirical work is needed to assess the general plausibility of the premise that nest-founding females experience higher condition-dependent variability in reproductive success than males. In scenarios where males face intense male–male competition [37] or where post-insemination sperm survival is highly dependent on male quality [38], this asymmetry may be lessened or even reversed. Conversely, conditions in which body condition appears to affect female fitness profoundly have been repeatedly documented [27,31,32,39–41]. The hypothetical effects of female-biased condition-dependence in nest-building insects raise several empirical questions. First, is condition-dependence more acute at temperate latitudes, where females can be filtered for quality by hibernation [31]? Second, does variable maternal condition at reproduction lead to Trivers-Willard effects [25,26], altering indirect fitness payoffs for female helpers? Third, do mothers face quantity–quality trade-offs in the brood, favouring smaller broods before helpers evolve in order to ensure sufficient per-capita resources fall on daughters to sustain competitiveness? Fourth, does the limited help received by first-emerging

daughters lead to a relatively 'subfertile' class [42] for whom altruism is the best available option? Fifth, when benefits of altruism arise through boosting sibling quality, to what extent does any redundant resource consumption by males (having less need than females) act as a constraint on the evolution of altruism in general, regardless of ploidy? Lastly, does load-lightening by first helper brood compensate for poor condition in foundress females, reducing the importance of female condition as sociality evolves?

In summary, we highlight a simple effect capable of promoting higher levels of altruism in haplodiploids than in diplodiploids without requiring split sex ratios [8], sex differences in helping efficiency [22], or strategic targeting of help to one sex in the brood [18]. Our aim is not to challenge the plausibility of sister-biased helping at the origin of eusociality, but rather to highlight that – contrary to a prevailing consensus – such a bias is not vital for the haplodiploidy hypothesis.

Figures:

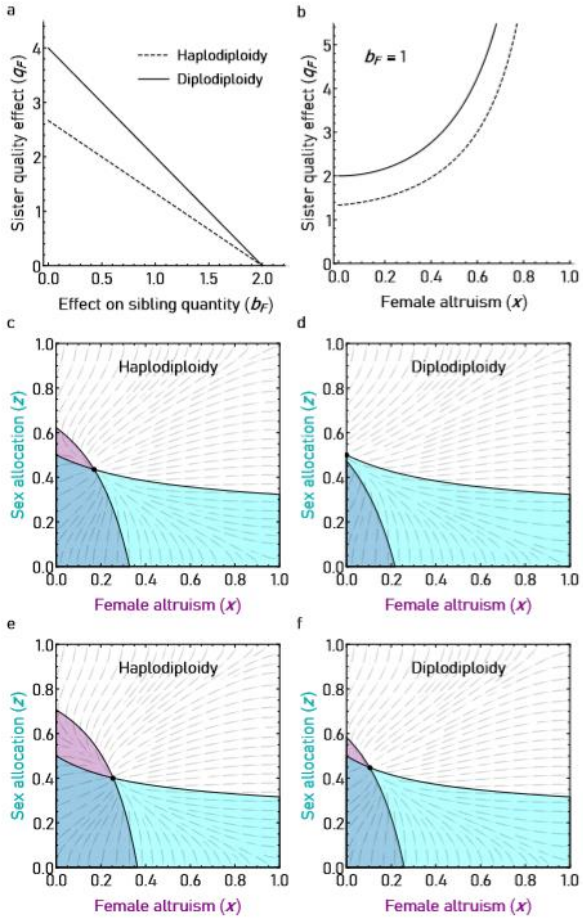

Fig. 1: When help raises the future quality of larval sisters especially, haplodiploid females are more prone to altruism than diplodiploids. (a) Threshold number (required for the invasion of altruism) of additional nieces and nephews from improved quality of sisters by a focal female becoming a sterile altruist in a nonsocial population ($\bar{x} = \bar{y} = 0$) with an equal sex ratio ($\bar{z} = \frac{1}{2}$), for different effects on the quantity of siblings (b_{F}). **(b)** The threshold effect on sister quality for further female altruism (x) as altruism rises in the population. The plotted line is found by setting the value of the candidate convergence-stable sex allocation $\bar{z}$ to that which corresponds to altruism level $\bar{x}$. Results are shown for $b_{\mathrm{F}} = 1$ as an illustrative value. **(c-d)** Increased sex allocation to males is favoured in the blue area; increased female altruism is favoured in the purple areas. Dots denote endpoint equilibria. As female altruists evolve, mothers bias the sex ratio towards the more helpful sex (females). Here, haplodiploids evolve helpers whilst diplodiploids do not. We plot results for linear relationships between helping (h) and quantity (B) and quality (Q), where $B = \alpha_B + \beta_B h$ (for $\alpha_B = 0.5$ and $\beta_B = 0.2$) and $Q = \alpha_Q + \beta_Q h$ (for $\alpha_Q = 0.05$ and $\beta_Q = 0.15$). **(e-f)** Raising the effect on sister quality ($\beta_Q = 0.2$) allows helpers to evolve in diplodiploids, but boosts altruism further in haplodiploids.

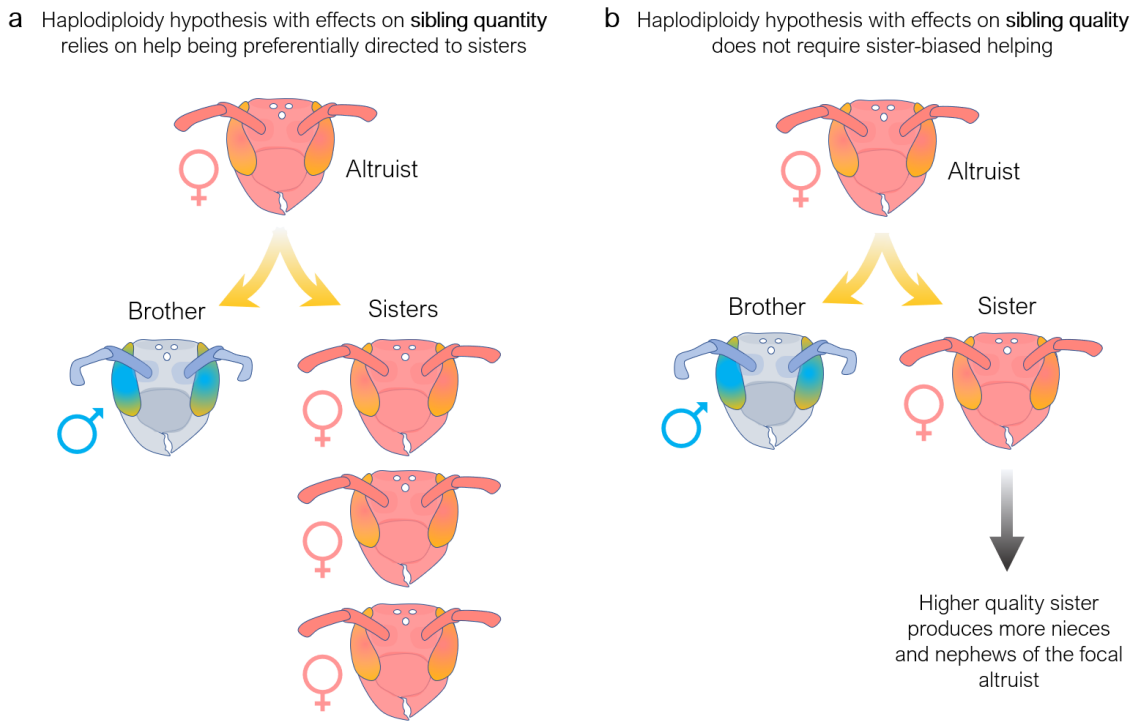

Fig. 2: Two routes to eusociality. (a) The classic view of altruism is that it increases sibling quantity. (b) Altruism may also increase sibling quality, especially benefitting nest-building females.

Acknowledgements

We are grateful to N. Davies, P. Rautiala, A. Higginson, T. Linksvayer, R. Bonduriansky, and an anonymous reviewer for comments, and to N. Davies for suggesting an intuitive measure of nieces and nephews. This work was supported by ERC Consolidator Grant 682253 (to ANR).

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Supplementary Information (*Sibling quality and the haplodiploidy hypothesis*)

We use the approach of Davies *et al.* [1], allowing a comparison with previous results. Key notation is summarized in Supplementary Table S1. Female absolute fitness w_{F} equals the probability that an egg develops as a female (where z is the probability of developing as a male, *i.e.* the maternal sex ratio) multiplied by the probability of developing as a reproductive (where x is the probability of developing as a sterile altruist), multiplied by fitness effects:

$$w_{\mathrm{F}} = (1-z)(1-x)B(h)Q(h) \tag{1}$$

We include two fitness effects: the probability $B(h)$ that the focal female survives to reach reproductive maturity; and the probability $Q(h)$ that she successfully founds a new nest given that she has reached reproductive maturity. This is a female-specific trait, affected by the amount of help (h) she receives before reproductive maturity. Average female absolute fitness is:

$$\bar{w}_{\mathrm{F}} = (1-\bar{z})(1-\bar{x})B\left(\bar{h}\right)Q\left(\bar{h}\right) \tag{2}$$

$B\left(\bar{h}\right)$ and $Q\left(\bar{h}\right)$ denote the averages in the population. Likewise, $\bar{z}$ and $\bar{x}$ are the population-average values of z and x respectively.

We assume an outbreeding population. y is the probability with which a male develops as a sterile altruist (with a population-average value of $\bar{y}$). As males do not found nests, we let male absolute fitness w_{M} depend only on the probability of reaching reproductive maturity ($B(h)$), the expected probability that a mate will successfully found a new nest ($Q(\bar{h})$), and the ratio of reproductively active females to males:

$$w_{\mathrm{M}} = z(1-y)B(h)Q\left(\bar{h}\right)\frac{(1-\bar{z})(1-\bar{x})}{\bar{z}(1-\bar{y})} \tag{3}$$

Average male absolute fitness is:

$$\bar{w}_{\mathrm{M}} = \bar{z}(1-\bar{y})B\left(\bar{h}\right)Q\left(\bar{h}\right)\frac{(1-\bar{z})(1-\bar{x})}{\bar{z}(1-\bar{y})} = \bar{w}_{\mathrm{F}} \tag{4}$$

Male and female relative fitnesses are $W_{\mathrm{M}} = \frac{w_{\mathrm{M}}}{\bar{w}_{\mathrm{M}}}$ and $W_{\mathrm{F}} = \frac{w_{\mathrm{F}}}{\bar{w}_{\mathrm{F}}}$. We follow Davies *et al.* [1] in defining help $h = (1-z)e_{\mathrm{F}}X + ze_{\mathrm{M}}Y$ as the sum of help from male and female helpers, where e denotes helping efficiency. Capitalised traits denote the local average value of the trait in a focal individual's group: X and Y are the average levels of female and male sterile altruism (respectively) in the focal individual's colony (e.g., the expected strategies of their siblings). We let $b_{\mathrm{F}} = e_{\mathrm{F}}\frac{\frac{dB}{dh}|_{h=\bar{h}}}{B(\bar{h})}$ denote the

fitness effect of female help on brood survival to reproductive maturity, and $q_{\mathrm{F}} = e_{\mathrm{F}} \frac{\frac{dQ}{dh}|_{h=\bar{h}}}{Q(\bar{h})}$. denote the fitness effect of female help on female nest-founding success.

Table S1: Notation

$B = B(h)$	Probability with which an egg survives to reach reproductive maturity. Helper siblings may raise this probability, increasing the quantity of siblings.
$Q = Q(h)$	Probability with which a reproductively-mature female successfully founds a nest (her 'quality'). Helper siblings may raise this probability by provisioning the female when she was a juvenile, increasing the quantity of nieces and nephews in the future.
x	Probability with which a female becomes a sterile helper. The population average value is $\bar{x}$.
y	Probability with which a male becomes a sterile helper. The population average value is $\bar{y}$.
z	Sex allocation (controlled by the mother). Following Davies et al. (2016), we assume that a mother produces a large number of eggs, of which a proportion z are male. The population average value is $\bar{z}$.
p	Consanguinity
b	Effect of help on $B(h)$ relative to the population average level $B(\bar{h})$, i.e. $b = e\frac{\mathrm{d}B/\mathrm{d}h}{B(\bar{h})}$. When females are helping, we denote this b_{F}, with $e = e_{\mathrm{F}}$ When males are helping, we denote this b_{M}, with $e = e_{\mathrm{M}}$
q	Effect of help on $Q(h)$ relative to the population average level $\mathrm{Q}(\bar{h})$, i.e. $q = e\frac{\mathrm{d}Q/\mathrm{d}h}{Q(\bar{h})}$. When females are helping, we denote this q_{F}, with $e = e_{\mathrm{F}}$When males are helping, we denote this q_{M}, with $e = e_{\mathrm{M}}$
e	Efficiency of help provided by each sex (e_{F} for females and e_{M} for males).
c_{F}	Class reproductive value of females for juveniles in the current cohort
c_{M}	Class reproductive value of males for juveniles in the current cohort
N	Population size
q_{HapF}	Threshold effect on sibling quality required for altruism by haplodiploid females
q_{DipF}	Threshold effect on sibling quality required for altruism by diplodiploid females

Female altruism

A neighbour-modulated model [2] looks at the fitness effects of a trait of interest on focal recipients, weighted by the relatednesses to actors bearing the traits. If a focal individual has a heritable trait value x, selection favours a higher value of x if an increase in their value of x is associated with an increase in their relative fitness W:

$$\frac{\mathrm{d}W_{\mathrm{focal}}}{\mathrm{d}x_{\mathrm{focal}}} > 0 \qquad (5)$$

Males and females may differ in their class reproductive values (c_{M} and c_{F}). For instance, in haplodiploids, a randomly sampled gene in the distant future is twice as likely to have been in a female in the current generation than in a male, so female class reproductive values are twice as large in

389 females as they are in males in haplodiploids ($c_{\mathrm{F}} = \frac{2}{3}$, $c_{\mathrm{M}} = \frac{1}{3}$, or – equivalently – a relative value of 2
390 for females and 1 for males). This is not the case in diplodiploids, where both sexes have equal class
391 reproductive values ($c_{\mathrm{F}} = c_{\mathrm{M}} = \frac{1}{2}$). Making class reproductive values explicit, the condition for
392 selection can be expanded as:

393 $$c_{\mathrm{F}} \frac{\mathrm{d}W_{\mathrm{F}}}{\mathrm{d}x_{\mathrm{F}}} + c_{\mathrm{M}} \frac{\mathrm{d}W_{\mathrm{M}}}{\mathrm{d}x_{\mathrm{M}}} > 0 \qquad (6)$$

394 Here, W_{F} is the relative fitness of a focal female and W_{M} is the relative fitness of a focal male. The
395 genic values for the trait x are x_{F} in the focal female and x_{M} in the focal male. The neighbour-modulated
396 approach expands the fitness effects on the focal individuals to make explicit the effects of different
397 actors on their relative fitnesses. For instance, in the current scenario (focusing on female-specific
398 helping), the trait affects fitness via the female herself (with a trait value x_{F}) and via the trait value of
399 sisters in the local group (with an average of X):

400 $$\frac{\mathrm{d}W_{\mathrm{F}}}{\mathrm{d}x_{\mathrm{F}}} = \underbrace{\frac{\partial W_{\mathrm{F}}}{\partial x_{\mathrm{F}}}}_{\substack{Fitness\\effect}} \underbrace{\frac{\mathrm{d}x_{\mathrm{F}}}{\mathrm{d}x_{\mathrm{F}}}}_{\substack{Relatedness\\to\ self}} + \underbrace{\frac{\partial W_{\mathrm{F}}}{\partial X}}_{\substack{Fitness\\effect}} \underbrace{\frac{\mathrm{d}X}{\mathrm{d}x_{\mathrm{F}}}}_{\substack{Relatedness\\of\ sisters}} \qquad (7)$$

401 $$\frac{\mathrm{d}W_{\mathrm{M}}}{\mathrm{d}x_{\mathrm{M}}} = \underbrace{\frac{\partial W_{\mathrm{M}}}{\partial X}}_{\substack{Fitness\\effect}} \underbrace{\frac{\mathrm{d}X}{\mathrm{d}x_{\mathrm{M}}}}_{\substack{Relatedness\ of\\sisters\ to\ male}} \qquad (8)$$

402 As in Davies *et al*. [1], we substitute consanguinities (p) for relatedness (r), since $p \propto r$. Consanguinity
403 denotes the probability that a random allele in the social partner is identical by descent to a random
404 allele at the same locus in the actor [3]. Selection favours an increase in the trait value x if:

405 $$c_{\mathrm{F}} \left(\frac{\partial W_{\mathrm{F}}}{\partial x} p_{\mathrm{self|F}} + \frac{\partial W_{\mathrm{F}}}{\partial X} p_{\mathrm{sis|F}} \right) + c_{\mathrm{M}} \left(\frac{\partial W_{\mathrm{M}}}{\partial X} p_{\mathrm{bro|F}} \right) > 0 \qquad (9)$$

406 Assuming monogamy, haplodiploid consanguinities from a focal female are $p_{\mathrm{self|F}} = \frac{1}{2}$, $p_{\mathrm{sis|F}} = \frac{3}{8}$, and
407 $p_{\mathrm{bro|F}} = \frac{1}{4}$ [4]. Diplodiploid consanguinities are $p_{\mathrm{self|F}} = \frac{1}{2}$, $p_{\mathrm{sis|F}} = p_{\mathrm{bro|F}} = \frac{1}{4}$.

408 Evaluating with fitness components at their population averages [2], dividing both sides of the
409 inequality by $N(1 - \bar{z})$ where N is population size (to allow reproductive value to be expressed per
410 individual), and rearranging, selection favours a small rise in female helping when:

411 $$b_{\mathrm{F}}(1 - \bar{x})(1 - \bar{z}) v_{\mathrm{F}} p_{\mathrm{sis|F}} + q_{\mathrm{F}}(1 - \bar{x})(1 - \bar{z}) v_{\mathrm{F}} p_{\mathrm{sis|F}} + b_{\mathrm{F}}(1 - \bar{y}) \bar{z} v_{\mathrm{M}} p_{\mathrm{bro|F}} > v_{\mathrm{F}} p_{\mathrm{self|F}} \qquad (10)$$

412 The indirect fitness benefits of developing as a sterile altruist are on the left-hand side of inequality
413 10. The direct fitness cost (the loss of the focal individual's own opportunity to reproduce, valued at

$v_{\mathrm{F}}p_{\mathrm{self|F}}$) is on the right-hand side. The actor's sacrifice results in $b_{\mathrm{F}}(1-\bar{x})(1-\bar{z})$ additional sisters, and an addition of nieces and nephews equal in value to $q_{\mathrm{F}}(1-\bar{x})(1-\bar{z})$ sisters.

We substitute the relevant consanguinities and class reproductive values into inequality 10. Holding q_{F} fixed, the threshold benefit level in terms of sibling quantity required to drive a small rise in helping by females of either ploidy occurs at:

$$b_{\mathrm{F}} = \frac{c_{\mathrm{F}}\left(p_{\mathrm{self|F}} - q_{\mathrm{F}}p_{\mathrm{sis|F}}(1-\bar{x})(1-\bar{z})\right)}{\left(c_{\mathrm{M}}p_{\mathrm{bro|F}} + c_{\mathrm{F}}p_{\mathrm{sis|F}}\right)(1-\bar{x})(1-\bar{z})} \tag{11}$$

Simplifying for haplodiploid females:

$$b_{\mathrm{HapF}} = \frac{1}{(1-\bar{x})(1-\bar{z})} - \frac{3}{4}q_{\mathrm{F}} \tag{12}$$

Simplifying for diplodiploid females:

$$b_{\mathrm{DipF}} = \frac{1}{(1-\bar{x})(1-\bar{z})} - \frac{1}{2}q_{\mathrm{F}} \tag{13}$$

Holding b_{F} fixed, the threshold benefit level in terms of sister quality required to drive a small rise in helping by females of either ploidy is (Fig. 1) occurs at:

$$q_{\mathrm{F}} = \frac{p_{\mathrm{self|F}}}{p_{\mathrm{sis|F}}(1-\bar{x})(1-\bar{z})} - b_{\mathrm{F}}\left(1 + \frac{c_{\mathrm{M}}p_{\mathrm{bro|F}}}{c_{\mathrm{F}}p_{\mathrm{sis|F}}}\right) \tag{14}$$

The values q_{HapF} and q_{DipF} in the main text are found by substituting the relevant consanguinities and class reproductive values for haplodiploids and diplodiploids respectively.

Male altruism

Next, we evaluate the costs and benefits of altruism (y) by males. Since we assume neither sex is superior in helping efficiency ($e_{\mathrm{M}} = e_{\mathrm{F}}$), the fitness effects of male help $b_{\mathrm{M}} = \frac{e_{\mathrm{M}}\frac{dB}{dh}}{\bar{B}}$ are equal to the fitness effects of female help ($b_{\mathrm{M}} = b_{\mathrm{F}}$). Selection favours male helping when:

$$c_{\mathrm{M}}\left(\frac{\partial W_{\mathrm{M}}}{\partial y}p_{\mathrm{self|M}} + \frac{\partial W_{\mathrm{M}}}{\partial Y}p_{\mathrm{bro|M}}\right) + c_{\mathrm{F}}\left(\frac{\partial W_{\mathrm{F}}}{\partial Y}p_{\mathrm{sis|M}}\right) > 0 \tag{15}$$

Solving for the fitness effects, selection favours a small rise in male altruism when, for both diplodiploid and haplodiploid males:

$$c_{\mathrm{F}}p_{\mathrm{sis|M}}\bar{z}(b_{\mathrm{M}} + q_M) + c_{\mathrm{M}}b_{\mathrm{M}}p_{\mathrm{bro|M}}\bar{z} > c_{\mathrm{M}}\frac{p_{\mathrm{self|M}}}{1-\bar{y}} \tag{16}$$

Dividing both sides by $N\bar{z}$, this can be rearranged to:

$$(b_{\mathrm{M}} + q_{\mathrm{M}})(1-\bar{z})(1-\bar{x})v_{\mathrm{F}}p_{\mathrm{sis|M}} + v_{\mathrm{M}}(1-\bar{y})\bar{z}b_{\mathrm{M}}p_{\mathrm{bro|M}} > v_{\mathrm{M}}p_{\mathrm{self|M}} \quad (17)$$

where individual reproductive values for males and females are (as above):

$$v_{\mathrm{M}} = \frac{c_{\mathrm{M}}}{N\bar{z}(1-\bar{y})}$$

$$v_{\mathrm{F}} = \frac{c_{\mathrm{F}}}{N(1-\bar{z})(1-\bar{x})}$$

Assuming monogamy, diplodiploid consanguinities from a focal male are $p_{\mathrm{self|M}} = \frac{1}{2}$, $p_{\mathrm{sis|M}} = p_{\mathrm{bro|M}} = \frac{1}{4}$, whilst haplodiploid consanguinities are $p_{\mathrm{self|M}} = 1$, $p_{\mathrm{sis|M}} = \frac{1}{4}$, and $p_{\mathrm{bro|M}} = \frac{1}{2}$.

Substituting in the relevant consanguinities:

$$\bar{z}\left(b_{\mathrm{M}} + \frac{q_{\mathrm{M}}}{2}\right) - \frac{1}{1-\bar{y}} > 0 \quad (18)$$

Holding q_{M} fixed, the threshold benefit level in terms of sibling quantity required to drive a small rise in helping by males of either ploidy is:

$$b_{\mathrm{HapM}} = b_{\mathrm{DipM}} = \frac{1}{\bar{z}(1-\bar{y})} - \frac{q_{\mathrm{M}}}{2} \quad (19)$$

Likewise, holding b_{M} fixed, the threshold benefit level in terms of sister quality required to drive a small rise in helping by males of either ploidy is:

$$q_{\mathrm{HapM}} = q_{\mathrm{DipM}} = \frac{2}{\bar{z}(1-\bar{y})} - 2b_{\mathrm{M}} \quad (20)$$

Sex allocation

An increase in sex allocation (i.e., to males) is favoured when [1]:

$$c_{\mathrm{F}}\frac{\partial W_{\mathrm{F}}}{\partial z}p_{\mathrm{dau}} + c_{\mathrm{M}}\frac{\partial W_{\mathrm{M}}}{\partial z}p_{\mathrm{son}} > 0 \quad (21)$$

In diplodiploids, $p_{\mathrm{dau}} = p_{\mathrm{son}} = \frac{1}{4}$, whilst, in haplodiploids, $p_{\mathrm{dau}} = \frac{1}{4}$ and $p_{\mathrm{son}} = \frac{1}{2}$ (assuming an outbreeding population) [1]. We let males and females be equally efficient potential helpers ($e_{\mathrm{M}} = e_{\mathrm{F}}$), such that q_{M} is equal to q_{F} and b_{M} is equal to b_{F}, and evaluate with traits at their population averages. An increase in sex allocation is favoured under either ploidy if:

$$(\bar{y}-\bar{x})(2b_{\mathrm{F}} + q_{\mathrm{F}}) - \frac{1}{1-\bar{z}} + \frac{1}{\bar{z}} > 0 \quad (22)$$

We solve for candidate convergence-stable values by setting the left-hand side equal to zero and rearranging for $\bar{z}$. The candidate value occurs at:

$$\bar{z} = \frac{2}{2 + \sqrt{4 + (2b_{\mathrm{F}} + q_{\mathrm{F}})^2(\bar{x} - \bar{y})^2} + (2b_{\mathrm{F}} + q_{\mathrm{F}})(\bar{x} - \bar{y})} \tag{23}$$

To generate Fig. 1b in the main text, we plot the thresholds for q_{F} (equations 2 and 3 in the main text) with $\bar{z}$ set to its candidate convergence-stable value, since $\bar{z}$ is expected to evolve as helpers invade the population due to mothers biasing the sex ratio towards the more helpful sex.

References in Supplementary Information

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